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THE MIGRATORY HABIT OF HOUSEFLY LARVÆ AS INDICATING A FAVORABLE REMEDIAL MEASURE. AN ACCOUNT OF PROGRESS.

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INTRODUCTION.

In the proceedings of the third meeting of the General Malarial Committee held at Madras in November, 1912, there is given a summary of a paper on "Insect Psychology" by Prof. L. M. Howlett. From his experiments with fruit flies, the stable fly, and mosquitoes he comes to the conclusion that "we must regard insects not as intelligent beings consciously shaping a path through life, but as being in a sort of active hypnotic trance." Also, that "once we discover the stimuli or particular conditions which determine a mosquito's actions we hold the key to the position, since we can then apply our knowledge to the mosquito's undoing." The second statement might have been made as general and inclusive as the first. One often hears expressed a general proposition to the effect that the problem of the control of any insect is very largely a problem of its behavior. If its habits are known, some means of control are usually not far to seek. Thus in the warfare against the common housefly there are two important lines of attack based on a knowledge of the habits of the adults. In the first place, advantage is taken of their feeding and drinking habits in the use of such things as sour milk, formalin and milk, beer and sugar, the fly poisons, etc., as bait for traps or as poisons. Secondly, a knowledge of the egg-laying habits of the female leads to the use of covered fly-tight receptacles for manure, garbage, or other fermenting material. Both of these methods are based on a knowledge of the habits of the adults. The question now presents itself, Is there any phase of the behavior of the larvæ which may afford a line of attack? Do they have any characteristic habit of which advantage may be taken in attempts to destroy them?

THE MIGRATORY HABIT

One need make only a few observations on the behavior of housefly larvæ to discover an excellent example of what Prof. Howlett calls "a sort of active hypnotic trance." This is to be found in the migratory habit which is so much in evidence during the prepupal stage. The habit has long been known and repeatedly mentioned in the literature. Thus Newstead (1907)[1] found that "deep down at the sides, in the cooler portions of the receptacles, the pupa or chrysalis stage occurred in enormous numbers, looking like small heaps or collections of reddish berries."

Griffith (1908) found that "the larvæ remained in the hottest part of the heap, but the pupæ were all found near the surface where it was cooler."

Jepson (1909), in certain rearing experiments in which moist bread was used as food, found that "the larvæ rarely left their feeding ground till fully fed, when they left the moist mass of bread for the surrounding dry area and there pupated."

Herms (1911) states that "the growing stage requires from four to six days, after which the maggots often crawl away from their breeding places, many of them burrowing into the loose ground just beneath the manure pile, or crawling under boards or stones or into dry manure collected under platforms or the like. * * * The larvæ often pass three or four days in the prepupal or migrated stage before actually pupating."

R. I. Smith (1911) says "it was very apparent that the maggots which swarmed through the manure were inclined to congregate in certain corners or crevices and pupate in a mass. * * * Scattered pupæ were discovered around the edges of the piles of cow manure and even in the soil underneath where the maggots had burrowed before pupating."

Hewitt (1912) states that "when full grown the mature larva usually leaves the moist situation in which it has developed for one of a drier nature, often crawling for several yards in search of some dry and sheltered crevice. Here it rests for a short time preparatory to changing into the pupal stage."

If any further evidence were needed to demonstrate such an habitual mode of action I might mention the following observations: During the past few months it has been my duty to assist in carrying out an extensive series of experiments in testing the value of various chemicals in treating manure with a view to the destruction of the larvæ present. The manure is placed in large cages and the chemical to be tested is sprinkled over it. The bottom of the cages consists of a galvanized iron pan with sides 1 foot high. In the floor of the pan are nine small holes. The sides of the cages above the

[1] Numbers in parentheses refer to dates in the bibliography, p. 11.

pan are of two layers of screen wire 2 inches apart. Now it was found in the very first experiments that larvæ were escaping from the cages, and it was seen that they found their way out through the holes in the floor of the cages and also through the screens at the sides. The numbers so escaping were surprising. It often happened that several hundred crawled out of the cage during 24 hours. They were found in the vessels placed beneath the cages to catch any drippings. By day the light was sufficient stimulus to prevent them from crawling out at the sides, but at night they were actually seen, with the aid of a flash light, making their way through both thicknesses of screen wire and dropping into the vessel below.

Moreover, in examining manure heaps on the open ground I have many records showing this "tendency to congregate" at the edges of the piles near the ground. About two cartloads of horse manure had been piled out on the open ground for five or six days during August, and at the end of this time it was hauled away. I examined the ground where the heap had been and found many pupæ, not in the center of the area formerly covered by the heap, but around the margin. Some were found on the surface, doubtless shaken out of the manure at the time of removal; others were found buried a half inch or more in the soil, where the larvæ had burrowed just previous to pupation.

In another case some 50 cubic feet of manure had been heaped up in a pile the base of which covered an area about 4 feet square. After the pile had stood three days larvæ were found swarming in the warm, moist parts of the heap near the top and some distance in from the sides. After eight days the entire pile was torn apart and gone over carefully in search of pupæ. None was to be found in the upper parts of the heap where I had previously seen great numbers of larvæ. In fact none was found until the very lowest layers were exposed. Here about 9,000 were collected. Not more than 100 were found below the soil. The mass of pupæ were scattered in little heaps about the margin. They were just outside the moist area of the manure, yet sufficiently protected from drying and sunlight by the overhanging straw. The explanation of their presence in such a position is, of course, that the larvæ, just before pupating, had migrated from the moist feeding grounds to a drier region more favorable to the resting stage. The examination of many other piles of manure showed the very same conditions existing, the only difference being in the number of pupæ collected.

Altogether some 50 or more heaps of manure on open ground have been examined. Each one contained from 40 to 50 cubic feet of manure. Some contained much long straw, others very little straw or bedding of any kind. The puparia are not hard to find nor hard to collect because of their occurrence in masses at the

edges of piles. Here are some of the figures obtained from a count of the pupæ collected from different piles: 7,000, 1,500, 10,000, over 12,000, 4,500, 6,000, 6,700, 30,000, etc.

In a recent article in the American Journal of Public Health, Levy and Tuck make the following statement: "We therefore announce the biological fact that the house fly does not pupate in manure if the full-grown larvæ can find any means of reaching and entering the earth." They claim that "the adult larvæ *regularly* leave the manure heap" and that they "enter the earth whenever it is possible for them to do so." To be sure, larvæ may and often do burrow into the ground before pupating—witness Dr. Terry's observations at Jacksonville, Fla., where he found larvæ and pupæ in the ground of soil-floor stables—but that they do so *regularly* is open to serious question. The figures given above are for puparia collected *above the surface* of the ground and *in the manure*. After the removal of the heaps, examination of the ground revealed only a very small percentage beneath the surface. The fact that some were found there shows that it was not the compact nature of the soil which prevented the majority from burrowing and that there was no reason why all could not have done so if such were their regular habit. It would seem that Levy and Tuck have put too much emphasis on this one point. A broader view, including all the phases of the migration of these creatures, is necessary and will not detract from the importance or value of the "maggot trap" which they have devised.

It is quite certain that the migrating habit is deeply ingrained and highly characteristic of housefly larvæ. A consideration of the known facts in the case will enable one to draw some inferences as to "the stimuli or particular conditions" which determine this mode of action. It has been noted that a sort of "wanderlust" seizes the larvæ just before pupation. It must be, therefore, that the migration is initiated in response to internal stimuli incident to the maturing of the larval stage and the onset of the metabolic changes preparatory to the transformation to the pupal stage. The course and direction of their travels are determined largely by external stimuli. It is quite evident that as pupation draws near they flee the very moist regions of a manure heap and seek the comparatively dry regions. If no such dry places are to be found in the manure, they will leave it to pupate in the ground or in cracks or crevices, under boards or stones, in loose material of any kind. Dr. Terry found both larvæ and pupæ in the soil of dirt-floor stalls. The larvæ were found in that part of the floor kept moist by the urine, while the pupæ were found in a ring in the drier soil outside the moist center. Further proof that moisture acts as a stimulus in determining their choice of a place for pupation is given below.

It is well known that they avoid light, and the rapidity with which they disappear from view when exposed to light through the disturbing of their feeding grounds is a familiar sight. The observation mentioned in which larvæ were seen crawling out through the screened sides of cages at night, but never during the day, is a case in point.

They avoid the extremely hot portions of manure heaps. Thermometers inserted from 6 to 12 inches toward the center of a heap will register anywhere from 110° F. to 170° F., which, of course, would be fatal. The hotter the pile the nearer the surface are the larvæ to be found. They also avoid the moldy parts of the heap. They seek, as it were, the safety of the middle region between the heat and mold of the center and the exposure to sunlight and dryness of the exterior. Doubtless other conditions also have an influence in determining their actions.

The habit of seeking the comparatively dry regions near the edge of manure heaps at the time of pupation is an adaptation of great advantage in that the adult fly at the time of emergence is thus afforded an easy path to freedom. It prevents the drowning of the imagines and insures the quickest possible expansion and drying of the wings. At least this is the teleological explanation. Yet it can not be claimed that these are intelligent acts, nor that the future is consciously provided for. We have here indeed a "battalion of somnambulists" acting in blind response to various internal and external stimuli.

THE BEARING OF THE MIGRATORY HABIT ON THE PROBLEM OF CONTROL.

So far as I have been able to determine, Levy and Tuck were the first to take advantage of the migratory habit in an attempt to destroy the maggots. In their paper published in July, 1913, they report two experiments. In the first they placed manure in a barrel in the bottom of which several holes had been bored, with the result that on the following day thousands of maggots were found in the tub placed beneath, and the number seemed to increase for three days. In a second experiment the bottom of the barrel was replaced by stout wire gauze. The results of this trial are not given.

It was not until the beginning of November that I learned of their work, and it was near the end of the month before I had an opportunity of reading the article. I had already carried out two experiments during the summer at Arlington, Va., and others during the fall at Audubon Park, New Orleans, La. The possibility of taking advantage of the migrating habit was suggested to me by experience with larvæ escaping from cages used in other experiments. The results of the experiments were beyond my best expectations, and

in the hope that they may be of some interest to others they are here reported in some detail.

A large galvanized iron pan, measuring 5 by 3 feet, with sides 4 inches high, was made. In this stood a container on legs 8 inches high. This container measured 4 by 2 by 2 feet. The sides and bottom were of heavy wire, ¼-inch mesh, supported by a light wooden framework. Twelve cubic feet of manure well infested with eggs and larvæ were placed in this container and sprinkled with water. Water was also poured into the pan below to the depth of about 1 inch. Surrounding and covering both pan and container was a fly-tight inclosure made of a large cage, 6 by 6 by 6 feet. This prevented further infestation of the manure, and an arrangement of traps at the top of the cage made it possible to capture and keep a record of any flies that might emerge. At the time for the emergence of flies the sides of the cage were darkened with black cloth in order to drive the flies into the traps at the top. Each day the larvæ were collected from the pan and counted, and each day the manure in the container was sprinkled thoroughly with water and the pan was washed out and again partly filled with water to drown the larvæ which fell into it. The records of Experiment No. 1 are summed up briefly in Table I.

TABLE I.—*Migratory habit of housefly larvæ; Experiment No. 1.*

Date.	Larvæ collected from pan.	Flies from traps.	Date.	Larvæ collected from pan.	Flies from traps.
1913			1913		
Aug. 27	337	.....	Sept. 6	0	88
28	715	.....	7	.....	102
29	1,550	.....	8	.....	23
30	[1] 10,000	.....	9	.....	19
31	[1] 8,000	.....	10	.....	9
Sept. 1	2,160	.....	12	.....	5
2	670	3	15	.....	6
3	263	18			
4	[2]	8		23,999	303
5	304	22			

[1] Approximate. [2] Collected on following day.

A few flies at the time of emergence fell into the water of the pan and were drowned. Allowing for these and for the few which may have escaped from the cage during the opening and shutting of the door, the total number of flies may be placed at 350. It will be seen from these figures that out of a possible total of 24,350 24,000, or a little more than 98 per cent, were destroyed through the catching of the larvæ in the manner described.

A second experiment was started on September 16. The manure used was from the same source as in the first experiment and contained practically the same proportion of straw. The same amount was used, viz, 12 cubic feet. The only respect in which this experi-

ment differed from the first was in the fact that the manure in the container was not sprinkled with water at any time, except for a light shower on September 19 and another on September 22. Much of this rainfall failed to reach the manure in the container because of the covering of the cage. A comparison of the results of this experiment with those of the first indicate the importance of moisture as a stimulus.

TABLE II.—*Migratory habit of housefly larvæ; Experiment No. 2.*

Date.	Larvæ collected from pan.	Flies caught in traps.	Date.	Larvæ collected from pan.	Flies caught in traps.
1913			1913		
Sept. 17	15	.....	Sept. 30	.....	64
18	132	.....	Oct. 1	.....	80
19	168	.....	2	.....	125
21	894	.....	3	.....	52
22	427	.....	4	.....	78
23	35	.....	6	.....	84
24	0	.....	7	.....	44
27	.....	43	8	.....	22
28	.....	43			
29	.....	33		1,671	668

Allowing for the few larvæ and adults which may have escaped, the totals may be given in round numbers as 1,700 larvæ and 700 adults. Thus from a possible total of 2,400, 1,700, or about 71 per cent, were destroyed. In passing it is unnecessary to point out that here 700 flies *did* pupate in the manure in spite of the fact that they had every opportunity to leave it.

With the approach of cold weather the work against the housefly was transferred to the experiment station at Audubon Park, New Orleans, La. Some other experiments of a similar nature were carried out here with smaller containers and cages. The strong wire baskets of the kind commonly seen in markets and stores for the display of fruits and vegetables made first-rate "maggot traps." The baskets used were 16 inches in diameter and 16 inches high and stood on legs 9 inches high. A galvanized-iron pan 2 feet square was made for this to stand in, and over all this was placed a cage consisting of a light wooden framework covered with black cloth. The top of the cage was covered by boards in which was an opening for the attachment of flytraps.

The third experiment was started on November 13. The basket was filled with manure taken from stables on November 12. The manure, which contained very little straw or bedding of any kind, was packed firmly in the basket and sprinkled with 4 quarts of water. The iron pan below was partly filled with water. The cage with its traps was not put in place until November 18, thus exposing the manure to possible infestation for a period of five days. The manure was sprinkled daily as long as larvæ appeared.

TABLE III.—*Migratory habit of housefly larvæ; experiment No. 3.*

Date.	Larvæ collected from pan.	Flies caught in traps.	Date.	Larvæ collected from pan.	Flies caught in traps.
1913.			1913.		
Nov. 14	162	.....	Nov. 27	.....	3
15	656	.....	28	.....	2
16	1,950	.....	29	.....	2
17	2,650	.....	Dec. 1	.....	2
18	1,240	.....	2	.....	8
19	40	.....	3	.....	5
20	[1]	7	4	.....	6
21	12	0	5	.....	15
22	0	0	6	.....	10
23	0	0	7	.....	3
24	0	0			
25	0	4		6,710	69
26	.....	2			

[1] Collected on following date.

Out of a possible total of 6,779 there were destroyed 6,710 larvæ, that is to say, about *99 per cent* were destroyed before they reached the pupal stage.

The percentages obtained in these experiments clearly demonstrate the habitual nature of the migration. They also demonstrate the efficiency of the maggot trap which is designed to take advantage of this mode of action. The question immediately arises whether the trap which appears so successful in an experimental way on a small scale can be adapted to the handling of manure in a practical way and on a large scale. Every consideration points to the probability that it can and that it will afford "an additional weapon of great value." However, the final verdict as to the value of the maggot trap must wait upon the solution of certain practical problems. To point out some of these here is to suggest lines for further investigation.

(1) In the first place, there must be determined what form, size, and construction of trap will give the best results. The answer to this will depend largely on the particular conditions obtaining at any given stable, such as the amount of manure produced daily, the arrangements for drainage, etc. It will also depend on the answer to the following problems:

(2) How deeply may manure be heaped in a trap without interfering with the migration? It will probably be found that the depth will make little difference, provided that the manure is kept moist, and provided that avenues of escape are afforded at the sides as well as at the bottom. The importance of providing a way of escape at the sides was not taken into consideration by Levy and Tuck in their preliminary experiments.

(3) How long must manure be kept in a maggot trap before it is entirely free from larvæ? This is a very important question from a practical standpoint, and one will find scant suggestion as to the answer in the literature on the life history and habits. The housefly

breeds preferably in horse manure, but it has never been determined just how long a given lot of manure continues to be an attractive place for egg laying, nor for how long a period fly larvæ will continue to appear in it. It is obvious that the maggot trap would not be practical if the infestation of the manure were daily renewed for a long time. Under ordinary conditions the drying of the surface of a heap of manure probably limits the period of egg laying to the first day or two of exposure. But in a maggot trap the manure must be kept wet in order to insure the greatest amount of migration. Would not such a moist surface be daily reinfested and maggots continue to appear in the manure as long as any fermentation were in progress? As a matter of fact, the period of infestation appears to be rather short, and even under the most favorable conditions maggots will rarely be found in a given lot of manure after 10 or 12 days' exposure. In support of this claim some experimental data may be given here.

A fourth experiment was carried out in the same manner as experiment No. 3, except that no cage was used to cover the trap at any time. The manure in the basket was thus continuously exposed to flies and the surface was kept moist by daily sprinkling. The larvæ were removed from the pan each day and counted and the pan was again partly filled with water. The manure used was taken from stables on November 12 and the experiment started on the same date. Larvæ began to appear in the pan on November 13 and continued daily to the 24th, as shown in Table IV.

TABLE IV.—*Migratory habit of housefly larvæ; Experiment No. 4.*

Date.	Larvæ caught.	Date.	Larvæ caught.
Nov. 13	14	Nov. 20	1,040
14	2,230	21	560
15	[1] 6,000	22	465
17	[1] 5,000	23	140
18	2,530	24	36
19	2,070		

[1] Approximate.

The manure contained little straw or other bedding and was very attractive to the flies as evidenced by the heavy infestation (about 20,000 from a little more than a bushel of manure). Yet no larvæ were to be found in the manure after 12 days.

Examination of heaps of manure on open ground has shown in many cases that at the end of eight days only pupæ were to be found in the manure. Even in cases where the manure was especially attractive to the flies, by reason of active fermentation and the absence of straw, all were found to have reached the pupal stage by the tenth day. Any device for applying the principle of the maggot trap on a large scale must take this time factor into consideration.

(4) The disposal of the maggots is another practical consideration. If the larvæ were allowed to drop to the ground they would burrow into it to pupate there and nothing would be gained. It would be necessary to have some sort of vessel, e. g., a concrete basin, beneath the trap. This should have vertical sides and contain an inch or more of a weak disinfectant or of water covered with a film of oil. If such a basin were connected with a sewer or cesspool the maggots collecting in it could be flushed out each week without the necessity of handling them in any way and without any offensive decomposition.

That the maggot trap possesses certain advantages is obvious and ought to lead to many attempts to develop it along practical lines. Cheapness would be one of its strong points. Practically the only cost would be the initial one for the construction of the trap and of a basin or receptacle for catching and disposing of the maggots. Very little additional time or labor would be required in operating it. The sprinkling of the manure would be a very small part of the daily routine of removing the manure from the stables. Proper arrangements for the disposal of the maggots would require only a few minutes' attention at long intervals.

Incidentally it may be noted that the maggot trap offers a convenient and easy means to the investigator or teacher who wishes to collect coprophagous larvæ in large numbers. In the experiments just reported the larvæ of *Musca domestica* L. were the most numerous, but in addition there were also collected larvæ of *Stomoxys calcitrans* L., of Homalomyia, of certain Sarcophagidæ, and doubtless of others. The total numbers collected were so large that no attempt was made to determine the relative abundance of the various forms.

SUMMARY.

Observations and experiments show that the migratory habit is deeply ingrained and highly characteristic of housefly larvæ.

The migratory habit appears in the prepupal stage in response to various internal and external stimuli.

Of the external stimuli, moisture is perhaps the most important in determining the direction of their travels and the choice of a place for pupation.

The migratory habit is an adaptation of great advantage in that it insures to the issuing adult the easiest and quickest escape.

This deep-seated habit offers an important point of attack in the attempts to control the pest.

Experiments with maggot traps show that 98 or 99 per cent of the total number of larvæ can be made to leave the manure, provided it is kept moist. Even from comparatively dry manure as many as 70 per cent can be destroyed.

The development of the maggot trap into an efficient weapon in the warfare against the housefly involves the working out of certain practical points, viz, the size and structure of the trap, the time necessary to keep the manure in the trap to rid it of maggots, the disposal of the larvæ, etc.

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